

The earliest bivalves and their Ordovician descendants

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Abstract. Replicated shell microstructure in a specimen of *Fordilla troyensis* Barrande from the Early Cambrian of Greenland confirms a close relationship between *Fordilla* Barrande from the North Atlantic region and *Pojetaia* Jell from the Early Cambrian of Australia and China. These genera could either be stem-group bivalves which predated the last common ancestor of living members of the class or the earliest known representatives of the extant subclasses Isofilibranchia and Palaeotaxodonta. Two other bivalved molluscs from the Middle Cambrian of Australasia and Scandinavia (*Tuarangia* Mackinnon and *Pseudomyona* Runnegar) had D-shaped valves, a single central adductor muscle, and shells formed of foliated calcite. They have been interpreted as early pteriomorphian bivalves and also as bivalved monoplacophorans; each displays some features of larval bivalves but at shell sizes that are larger than is typical for bivalve prodissoconchs. If *Tuarangia* and *Pseudomyona* were early pteriomorphian bivalves the Class Bivalvia might well be diphyletic. However, it is more likely that the Palaeotaxodonta had a fordillid ancestor and that all other extant subclasses of Bivalvia were derived from this paraphyletic group. Other proposed genera of Cambrian Bivalvia (*Buluniella* Jermak, *Cycloconchoides* Zhang, *Hubeinella* Zhang, *Lamellodonta* Vogel, *Oryzoconcha* He and Pei, *Praelamellodonta* Zhang, *Xianfengoconcha* Zhang, *Yangtzedonta* Yü) are either not molluscs or are junior synonyms of *Fordilla* and *Pojetaia*.

The search for Cambrian ancestors of the bivalves that are so obvious in Ordovician epicontinental marine strata has yielded a variety of fossils that have been offered as early representatives of the Class Bivalvia (Table 1). Of these, only *Fordilla* Barrande (Pojeta, 1975) and *Pojetaia* Jell (Runnegar and Bentley, 1983) are regarded widely as true bivalves but even they could represent stem group taxa in that they could predate the latest common ancestor of all living members of the class (Morris, 1990; Waller, 1990). Two Middle Cambrian taxa, *Pseudomyona* Runnegar and *Tuarangia* Mackinnon (which are obviously related to one another), have been regarded as early pteriomorph bivalves by some workers (Mackinnon, 1982; Berg-Madsen, 1987) but Runnegar (1983) considered them to be bivalved monoplacophorans, analogous to living bivalved opisthobranch gastropods. The purpose of this brief review is to reassess the status of these four genera and their role in the early history of the class. All other proposed Cambrian Bivalvia are either junior synonyms of *Fordilla* and *Pojetaia* or are other kinds of fossils that have been mis-identified as bivalves (Table 1). The most notable of the latter kind is *Lamellodonta simplex* Vogel, which Havlíček and Kříž (1978) showed to be a deformed obolellid brachiopod.

BIOSTRATIGRAPHY OF CAMBRIAN BIVALVES

Both *Fordilla* and *Pojetaia* are middle Early Cambrian

in age. In South Australia, *Pojetaia runnegari* Jell occurs in three of four successive trilobite zones of the middle part of the Early Cambrian (zones of *Abadiella huoi* (Zhang), *Pararaia tatei* (Woodward) and *P. janeae* Jell; Bengston *et al.*, 1990). This stratigraphic range is approximately equivalent to the Chiungchussu and Tsanglangpu stages of the Chinese Early Cambrian succession and to the Atdabanian and Botomian stages of the Siberian Platform. Chinese occurrences of *Pojetaia* are from the early Tsanglangpu stage (Chen and Wang, 1985; He and Pei, 1985) and are probably equivalent in age to the zone of *Nevadella* Raw of North America (P. A. Jell, pers. comm.).

Fordilla is found in the middle Early Cambrian rocks in eastern North America, Greenland and Denmark (Pojeta, 1975) and in Tommotian and Atdabanian strata of the Siberian Platform (Jermak, 1986, 1988). There is no longer any evidence that the first appearance of *Pojetaia* predates significantly the origin of *Fordilla* (e.g. Jell, 1980); the two taxa probably originated at approximately the same time and then coexisted in different biogeographic regions (Redlichian and Olenellian realms; Kobayashi, 1972) for about 10 million years.

Tuarangia paparuia Mackinnon and *T. gravgaerdensis* Berg-Madsen occur in approximately coeval late Middle Cambrian (Boomerangian) strata in New Zealand and Denmark (Berg-Madsen, 1987). *Pseudomyona* is known only from its type locality in northwestern Queensland which is early Middle Cambrian (Floran) in age (Southgate, 1986).

Table 1. List of generic and specific names that have been proposed for fossils considered to be Cambrian bivalves (type species are identified by an asterisk). Only two Early Cambrian species (*Fordilla troyensis* and *Pojetaia runnegari*) are certainly bivalves. Our assessment of the remaining taxa, based in most cases upon an examination of original material, is given in the right hand column.

<i>Buluniella</i> Jermak, 1986	
<i>B. borealis</i> * Jermak, 1986	<i>Fordilla troyensis</i> ?
<i>Cycloconchioides</i> Zhang, 1980	
<i>C. elongatus</i> Zhang, 1980	stenotheceid
<i>C. venustus</i> Zhang, 1980	stenotheceid
<i>Fordilla</i> Barrande 1881	
<i>F. troyensis</i> * Barrande, 1881	Early Cambrian bivalve
<i>F. sibirica</i> Krasilova, 1977	<i>F. troyensis</i>
<i>Hebeinella</i> Zhang, 1980	
<i>H. formosa</i> * Zhang, 1980	stenotheceid
<i>Lamellodonta</i> Vogel, 1962	
<i>L. simplex</i> * Vogel, 1962	inarticulate brachiopod
<i>Oryzoconcha</i> He and Pei, 1985	
<i>O. prisca</i> * He and Pei, 1985	<i>Pojetaia runnegari</i>
<i>Pojetaia</i> Jell, 1980	
<i>P. ovata</i> Chen and Wang, 1985	<i>P. runnegari</i>
<i>P. runnegari</i> * Jell, 1980	Early Cambrian bivalve
<i>Praelamellodonta</i> Zhang, 1980	
<i>P. elegans</i> * Zhang, 1980	stenotheceid
<i>Pseudomyona</i> Runnegar, 1983	
<i>Myona queenslandica</i> * Runnegar and Jell, 1976	Middle Cambrian bivalve?
<i>Tuarangia</i> Mackinnon, 1982	
<i>T. paparua</i> * Mackinnon, 1982	Middle Cambrian bivalve?
<i>T. gravgaardensis</i> Berg-Madsen, 1987	Middle Cambrian bivalve?
<i>Xianfengconcha</i> Zhang, 1980	
<i>X. elliptica</i> Zhang, 1980	stenotheceid
<i>X. rotunda</i> Zhang, 1980	stenotheceid
<i>X. minuta</i> Zhang, 1980	stenotheceid
<i>Yangzedonta</i> Yü, 1985	
<i>Y. primitiva</i> * Yü, 1985	unique, unidentified microfossil

Berg-Madsen (1987) also illustrated a single specimen of *Tuarangia* from a glacial erratic in north Poland; the presence of the conodont *Westergaardodina tricuspida* Müller in the same boulder suggested an early Late Cambrian age for the source rock.

HIGHER TAXA OF CAMBRIAN BIVALVES

When Jell (1980) described *Pojetaia runnegari* he noted its similarities to *Fordilla troyensis* (size, shape, cardinal hinge teeth, opisthodontic ligament, etc.) and placed it in the same family (Fordillidae) and order (Fordilloida) as *Fordilla*. In contrast, Runnegar and Bentley (1983) emphasised similarities between *Fordilla* and Ordovician isofilibranch bivalves such as *Neofordilla* Krasilova and *Modiolodon* Ulrich and they therefore referred *Fordilla* to the Mytilacea. *Pojetaia*, on the other hand, was regarded as a primitive nuculoid palaeotaxodont. This interpretation placed the origin of these two

subclasses (Isofilibranchia and Palaeotaxodonta) within the Fordillidae during the Early Cambrian.

One of the most distinctive features of *Pojetaia* is seen on phosphatic internal molds of the shell (Figs. 1D-E). The surface of most internal molds is covered with imbricated polygonal cells that are inclined in a consistent way and become smaller toward the growing margin of the valve. These cells were interpreted as the impressions of the ends of near-vertical prisms formed of aragonite fibers by Runnegar and Bentley (1983) and Runnegar (1985), but this interpretation has been challenged by Carter and Clark (1985) and Carter (1990), who regard the structure as the imprints of exceptionally large (30 µm) tablets of nacre. Although we do not agree with this suggestion because nacre tablets are never imbricated, we must admit that the microstructure of the *Pojetaia* shell is not yet well understood.

Nevertheless, a clearly homologous microstructure was present in the *Fordilla* shell (Figs. 1A-B). A steinkern of *F. troyensis* discovered in Greenland by John S. Peel has the same kind of cellular network as internal molds of *Pojetaia*, except that in *Fordilla* the cells are more elongated than they are in *Pojetaia*. As in *Pojetaia*, each cell has closely-spaced transverse marks which could be casts of individual mineral (aragonite?) fibers.

The importance of this unusual shell microstructure is that it reunites *Fordilla* and *Pojetaia* into a monophyletic group (Fig. 2). Thus Waller (1990) treated this microstructure as an autapomorphy of the Fordilloida and, on that basis, regarded the fordillids as an extinct stem group which diverged from the line leading to modern bivalves prior to the origin of the class. In Waller's phylogenetic tree all modern bivalve higher taxa are derived directly or sequentially from Early Ordovician palaeotaxodonts.

It is unlikely that the distinctive shell microstructure of *Fordilla* and *Pojetaia* would be lost independently in lines leading to both the Palaeotaxodonta and the Isofilibranchia so the independent derivation of these subclasses from the Fordillidae is not supported by the new microstructural evidence. However, inclined (but near-vertical) aragonitic prisms of the type postulated by Runnegar and Bentley (1983) in *Pojetaia* have been observed in the outer shell layer of a Devonian nuculoid [*Palaeoneilo filosa* (Conrad); Carter, 1990: 159-162] and so it is still possible that the Early Ordovician palaeotaxodonts are direct descendants of a fordillid such as *Pojetaia*.

A quite different shell microstructure unites *Tuarangia* and *Pseudomyona* (Fig. 3G). Once again, this microstructure is known only from phosphatic replicas of the inner surfaces of recrystallized shells. It has been interpreted as replicated foliated calcite by comparison with modern examples and crystallographic analysis (Mackinnon, 1982; Runnegar, 1984); it must be a primary feature of the shell rather than a secondary diagenetic artefact for the foliated calcite

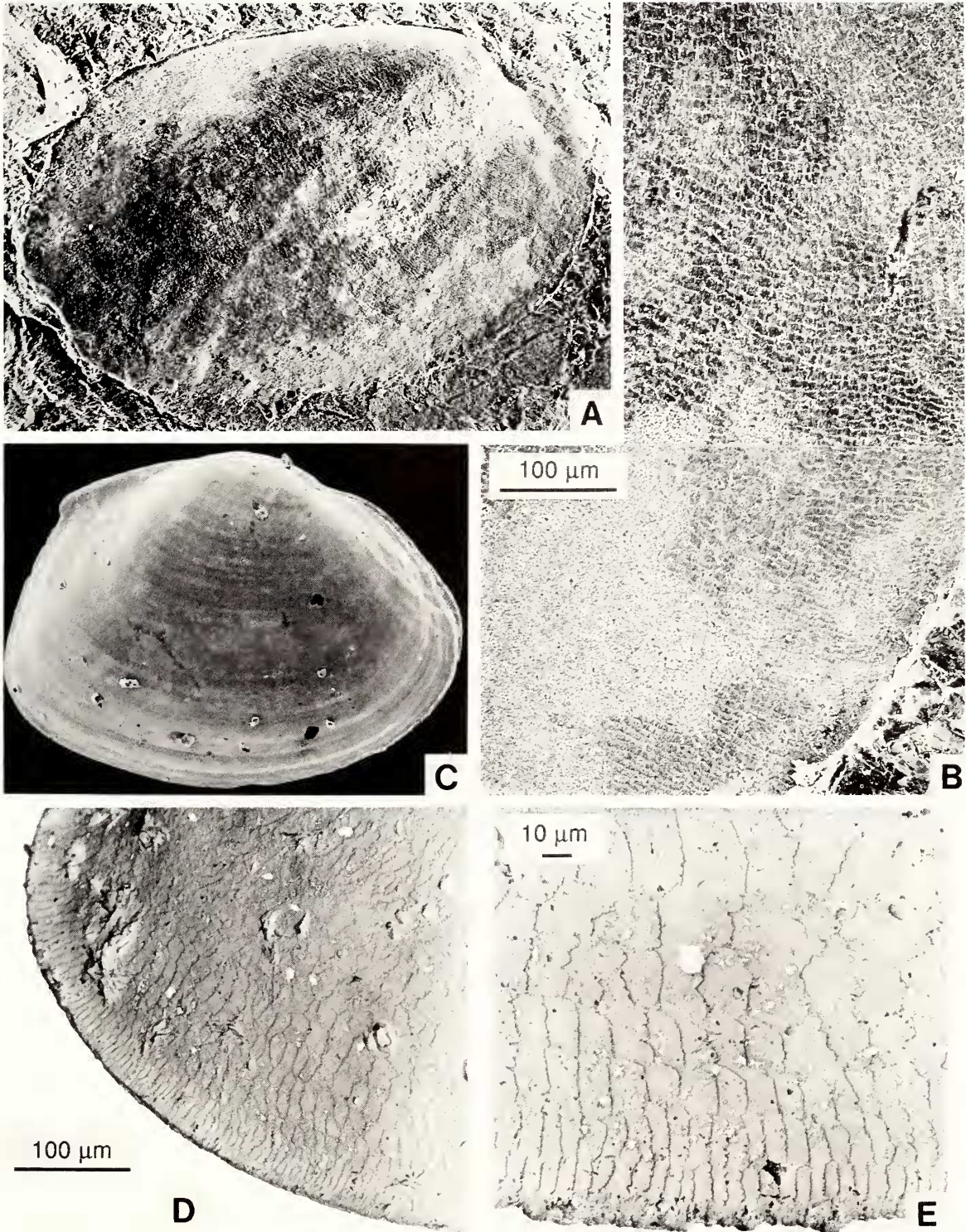


Fig. 1. Replicated shell microstructure of *Fordilla troyensis* Barrande (A-B) and *Pojetaia runnegari* Jell (C-E), Early Cambrian bivalves. **A**, dolomitic internal mold of right valve, Early Cambrian, Greenland, showing replicas of structures interpreted by Runnegar and Bentley (1983) as casts of the ends of composite prisms formed of fibrous aragonite (shell length = 3.25 mm). **B**, enlargement of antero-ventral part of A. **C**, exterior of right valve; shell is 1.0 mm long. **D-E**, scanning electron micrographs of the antero-ventral part of internal mold of right left valve; the images have been electronically inverted to give the impression of the actual structure rather than its negative cast.

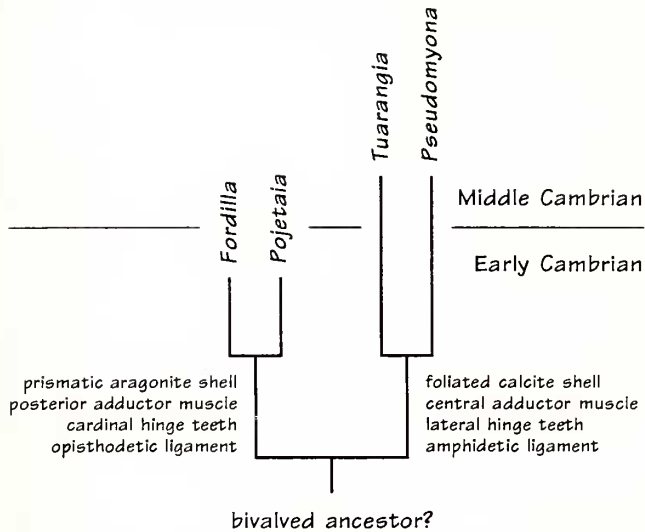


Fig. 2. Tree illustrating the phylogenetic hypotheses discussed in the text. It is concluded that *Fordilla* Barrande and *Pojetaia* Jell did not share a common bivalved ancestor with *Tuarangia* Mackinnon and *Pseudomyona* Runnegar.

stops abruptly at the edges of muscle scars (Fig. 3F) and the trend of the folia is related to their position along the valve margin (Runnegar, 1983). A similar microstructure has been observed in the Middle Cambrian snorkel-bearing univalve *Eotebenna* Runnegar and Jell (Runnegar and Jell, 1976; Runnegar, 1983) but is otherwise known from fossil molluscs until the (presumably independent) origins of foliated calcite in the patelloid limpets and pectinoid bivalves some time during the early post-Cambrian Paleozoic.

In addition to a foliated calcite shell, *Tuarangia* and *Pseudomyona* each had an amphidetic hinge, D-shaped valves and lateral but not cardinal teeth (Fig. 3). They both probably also possessed the central adductor muscle seen in *Pseudomyona* (Runnegar, 1983). However, it is not clear whether the "protoconch" of *Pseudomyona* (Figs. 3A, 3C-D) is homologous with the central "ligament pit" of *Tuarangia* (Fig. 3E).

Mackinnon (1982) and Berg-Madsen (1987) have regarded *Tuarangia* and *Pseudomyona* as early pteriomorphian bivalves belonging to the extinct Order Tuarangiida. They cited the amphidetic ligament, straight hinge, lateral teeth and foliated calcite shell as pteriomorphian characters. The problem with this interpretation is that this collage of characters is not characteristic of the early pteriomorphians so far discovered in Ordovician strata (Pojeta and Runnegar, 1985).

DISCUSSION

By the end of the Ordovician, at least five of the extant subclasses of bivalves had appeared: Palaeotaxodonta;

Isofilibranchia [Boss (1982) and Waller (1990) consider the Isofilibranchia to be a superorder of the Pteriomorphia]; Anomalodesmata; Heteroconchia; Pteriomorphia (Pojeta and Runnegar, 1985). On both stratigraphic and morphological grounds the palaeotaxodonts are regarded frequently as primitive and the direct or indirect ancestors of both the Pteriomorphia and the Heteroconchia (Palaeoheterodonta + Heterodonta) (Pojeta and Runnegar, 1985; Waller, 1990). It is possible (but less likely) that the nuculoid palaeotaxodonts were derived from an actinodont heteroconch (Babin and Gutiérrez-Marco, 1991).

Waller (1990) used the distinctive microstructure of *Pojetaia* and *Fordilla* as a synapomorphy for the Fordilloida, which he regarded as the sister group of the rest of the Bivalvia. He supported this taxonomic decision with the assumption that the fordillids had lost a preexisting nacreous inner shell layer and had not yet acquired a fibrous layer in their ligament. This allowed him to reinstate the palaeotaxodonts as the earliest members of the crown group. Morris (1990) came to a similar conclusion but for less explicit reasons.

Although some laterally-compressed Cambrian molluscs apparently had prismatic-nacreous aragonitic shells (Runnegar, 1985), there is no evidence that nacre was present in (or absent from) the ribeirioid rostroconch ancestors of the bivalves (Runnegar, 1983). Similarly, the ligaments of *Pojetaia* and *Fordilla* are not preserved and so could have been fibrous, granular or unmineralized; in any case, the ligament of nuculids is *not* fibrous and Waller (1990) has therefore suggested that the granular ligament of *Nucula* Lamarck is a derived condition. [Based on evidence obtained from well-preserved Devonian nuculoids, Carter (1990) also proposed that the granular ligament of *Nucula* is derived from an ancestral weakly-mineralized to non-mineralized condition.] Given these and other uncertainties we tentatively maintain the fordillids within the crown group for the time being. As mentioned above, it is possible that *Pojetaia* was an early palaeotaxodont.

Pojeta and Runnegar (1985) recognized four major kinds of Ordovician pteriomorphs: pterineid pteriaceans; cyrtodontids; ambonychiids; a probable ancestral limid, *Prolobella?* Ulrich. Under some existing classifications the pterineids and the limid would be placed together in the order Pterioidea but this grouping makes little sense in an Ordovician context because the pectiniform shell of *Prolobella?* is unlikely to be homologous with the shells of younger Pectinacea. We therefore agree with Waller (1978) and Johnston (1991) who assigned the ambonychiids and limoids to the superorder Prionodonta, *sensu* Boss (1982).

The duplivincular ligament of the pterineids, cyrtodontids, and ambonychiids strongly suggests that they constitute a monophyletic group (Prionodonta + Eupteriomorphia). Many authors have considered the cyrtodontids to

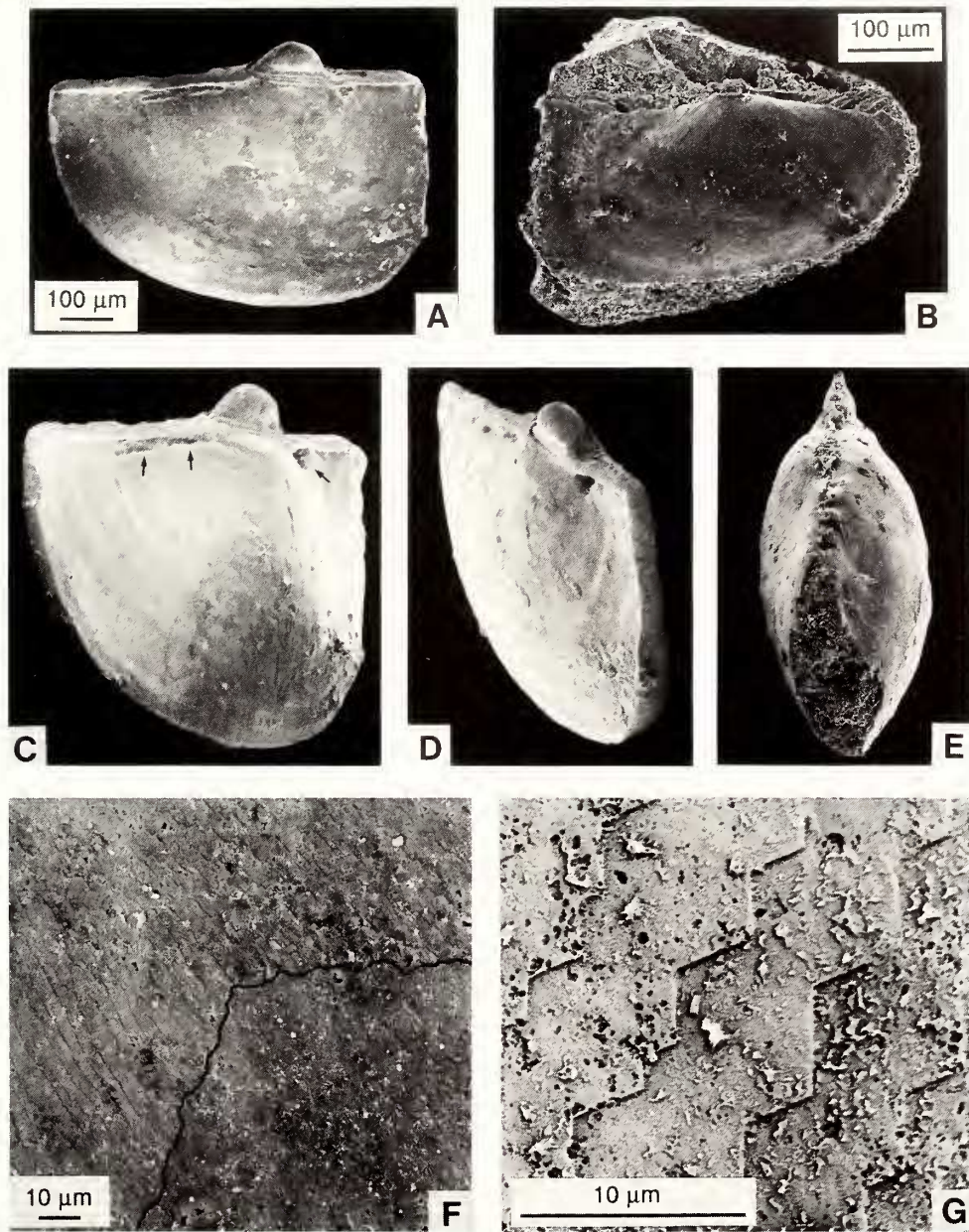


Fig. 3. Middle Cambrian bivalved molluscs, *Pseudomyona queenslandica* (Runnegar and Jell) (A, C-D, F-G) and *Tuarangia gravgaardensis* Berg-Madsen (B, E). **A, C-D**, phosphatic internal mold viewed from right? side and posterior? and anterior? ends, note lateral teeth (arrows) and univalved protoconch. **B**, internal mold of right? valve showing well-developed lateral teeth. **E**, end-on view of internal mold showing crenulations caused by interlocking teeth and central “ligament pit”. **F**, surface of internal mold showing casts of overlapping calcite folia (upper left), edge of adductor muscle scar (ink line), and smooth surface of adductor scar; polygons near edge of adductor scar are interpreted as casts of myostracal prisms. **G**, enlargement of replicated foliated calcite on surface of internal mold.

be the most primitive pteriomorphs and they derive them either from the cycloconch actinodonts (Pojeta and Runnegar, 1985; Johnston, 1991) or “actinodont” palaeotaxodonts (Waller, 1990). Johnston (1991) has described a Silurian eupteriomorph (*Umburra cinefacta* Johnston) which he regards as “more primitive dentally” than any known cyrtodontid. If this were true, then the common ancestor of the

prionodonts and the eupteriomorphs would have had an equivalved shell, a duplivincular ligament and “actinodont” hinge teeth. Although this hypothetical ancestor approximates some of the morphological features of *Tuarangia* and *Pseudomyona*, it almost certainly would have had anterior and posterior adductor muscles (Johnston, 1991) rather than the single central adductor muscle of *Pseudomyona* and a

nacreous or crossed-lamellar aragonitic shell (Carter, 1990) instead of the foliated calcite shell of *Pseudomyona* and *Tuarangia*. Thus the postulated genetic connection between *Tuarangia/Pseudomyona* and the Pteriomorpha (Mackinnon, 1982; Berg-Madsen, 1987) remains tenuous and is not supported by the evidence currently available. As there is no character apart from the bivalved condition in common between the fordillids and either *Pseudomyona* or *Tuarangia* it is difficult to sustain the hypothesis that they once shared a common bivalved ancestor (Fig. 2). On the contrary, the presence of foliated calcite in the pseudobivalved univalve *Eotebenna pontifex* Runnegar and Jell (Runnegar and Jell, 1976) is an indication that *Pseudomyona* and *Tuarangia* are not true bivalves and that the Class Bivalvia is therefore monophyletic.

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